MERA food web assembly: allowing for predation on different trophic levels (omnivory)

Jade, Jul 3

One artificial constraint in the current model is that each species can only prey on those in the next highest trophic level but not any lower levels. Here I relax this constraint by making it possible for a predator species to prey on species from all trophic levels lower than the one the predator is in. In this way, a species can be omnivore consuming potentially all other species and the fundamental resource.

In the following first I will show the case where species can prey on all other species but not the fundamental resource at the same time. Since the case where a species feed on both the fundamental resource and other species requires the specification of resource distinguishability (discussed before in write-up May 8: A more complete model for the multiple resource scenario of MERA), it will be shown separately in the second section.

In all graphs showing the food web structure, the fundamental resource is put on trophic level 0 so that the trophic links between the resource and species from all trophic levels can be shown.

1 Allowing species to prey across multiple trophic levels (not including the fundamental resource)

In this scenario, a new species can choose to prey on any subset of all other species already existing in the community OR the fundamental resource, but not at the same time. The algorithm to optimize the position of each new species is the same as before, just that instead of restricting potential prey to species at a certain trophic level each time, the potential prey set is all other existing species. The trophic level of the species will be one level higher than the highest trophic level of its prey.

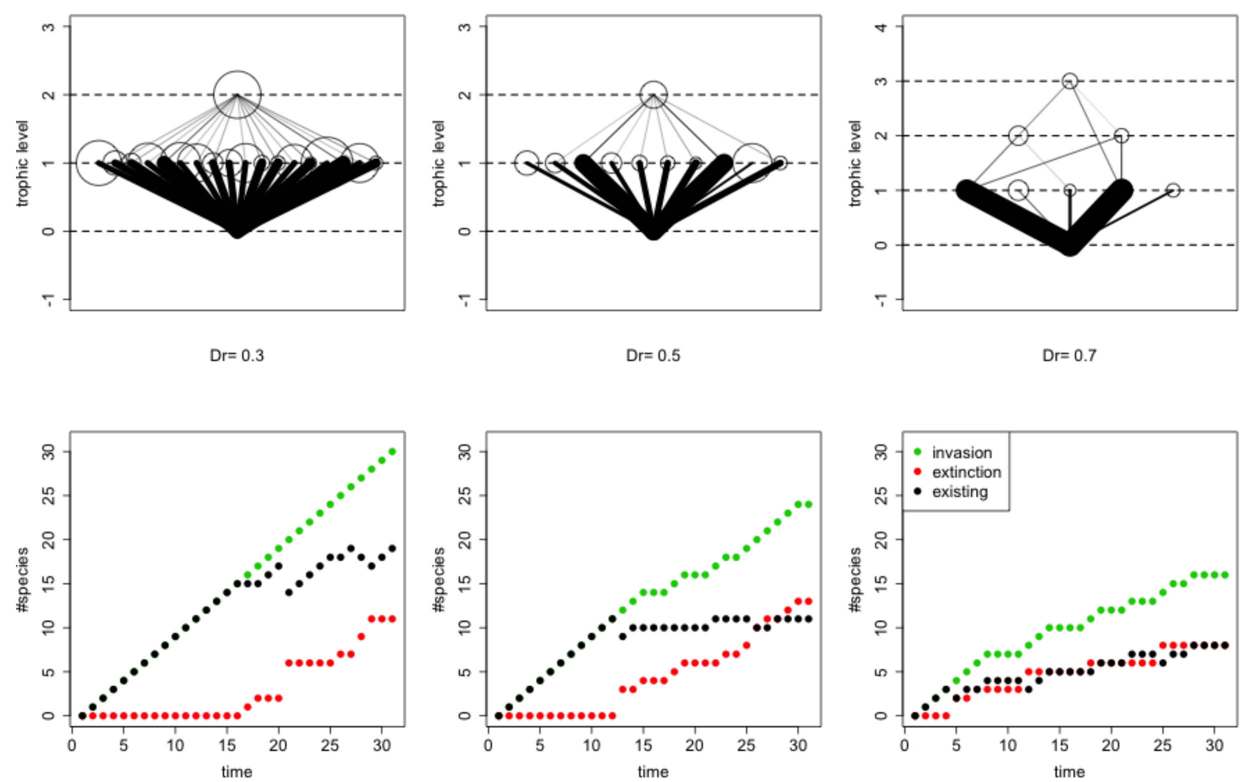

Fig. 1 D_r **effect for species-only predation (**$\gamma = 0.1$**,** D_r **from left to**

right is 0.3, 0.5 and 0.7)

As in the previous model, higher D_r leads to smaller number of species but more trophic levels (due to the higher competitiveness among species at the same level). Notice that when there are more than 2 trophic levels (as in the case $D_r = 0.7$), the species at higher levels can prey on not only the species at the next highest level, but also those at all lower levels.

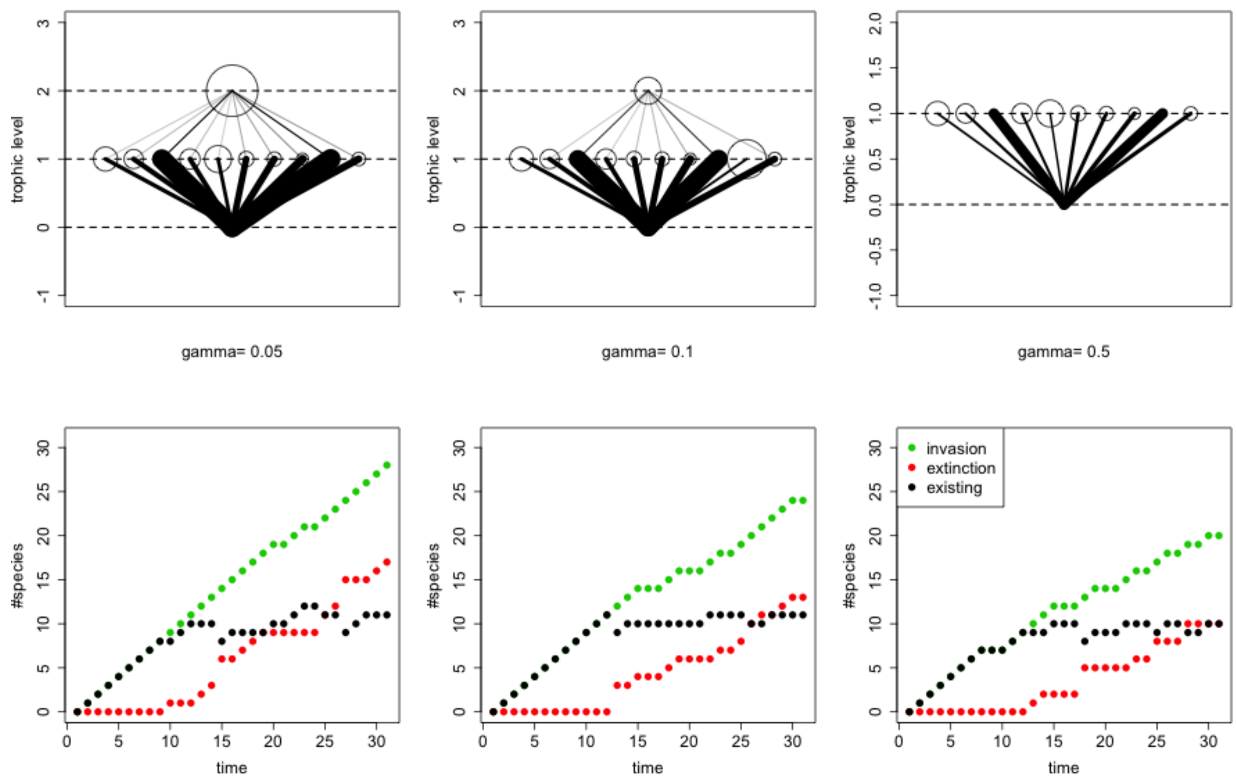

Fig. 2 γ effect for species-only predation ($D_r = 0.5$, γ from left to right is 0.05, 0.1 and 0.2)

Here the result also resembles that of the previous model: γ does not significantly affect the number of species, but a higher γ decreases the number of trophic links (due to the associated higher cost in having more preys).

2 Allowing species to prey on both other species and the fundamental resource at the same time

In this scenario a species can prey on any subset of all other species AND the fundamental resource. A resource distinguishability $D_{r,R} > 0$ is needed so that there is a cost in adding the fundamental resource as food (capture efficiency τ_c has to multiply $e^{-\gamma D_{r,R}}$) and so that not all species feed on the fundamental resource. Here I arbitrarily choose $D_{r,R} = 0.5$, the sensitivity to which can be tested.

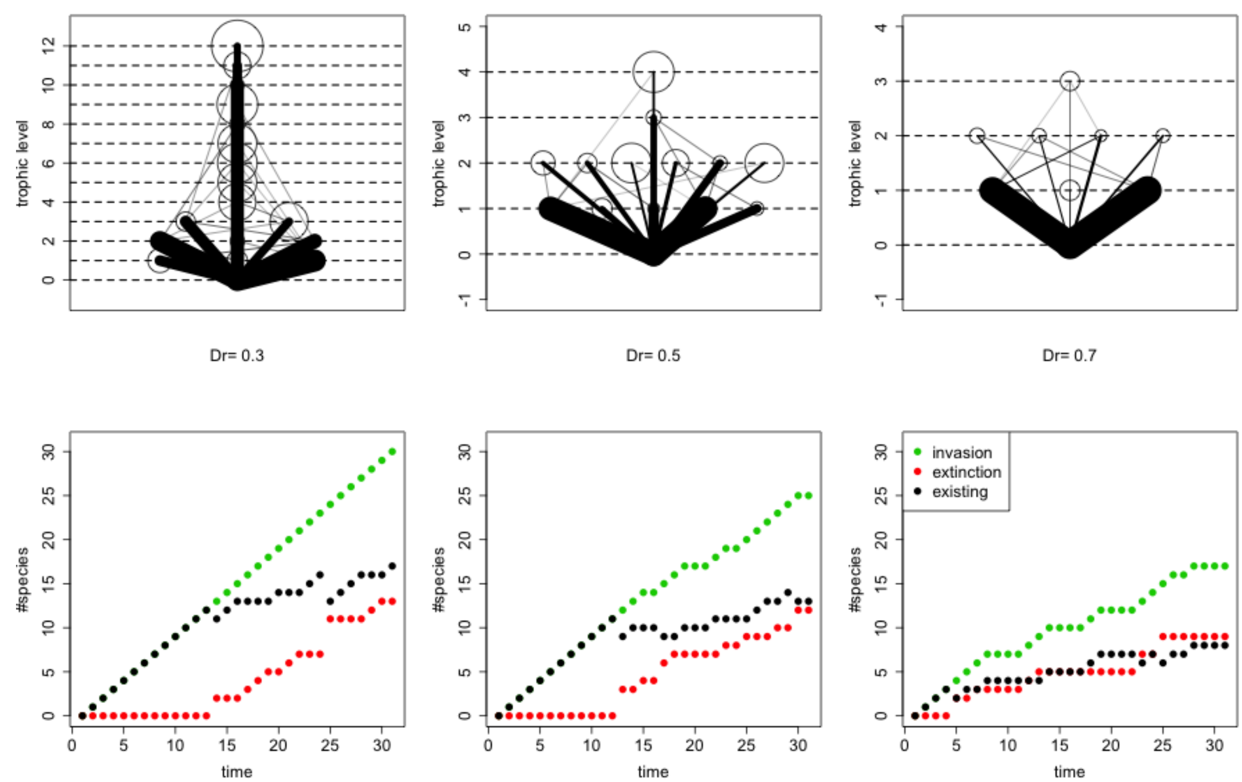

Fig. 3 D_r effect when species can feed on other species and resource simultaneously ($\gamma = 0.1$, D_r from left to right is 0.3, 0.5 and 0.7)

Here a higher D_r still leads to fewer species. However, as is opposite to the first case, the number of trophic levels also decreases with D_r. This is because that in this case, species from all trophic levels can feed on the fundamental resource while feeding on other species and therefore the comparative advantage of being on higher trophic levels is higher than when predation is restricted to species only. From the graph we can see that, almost all species are connected to the fundamental resource.

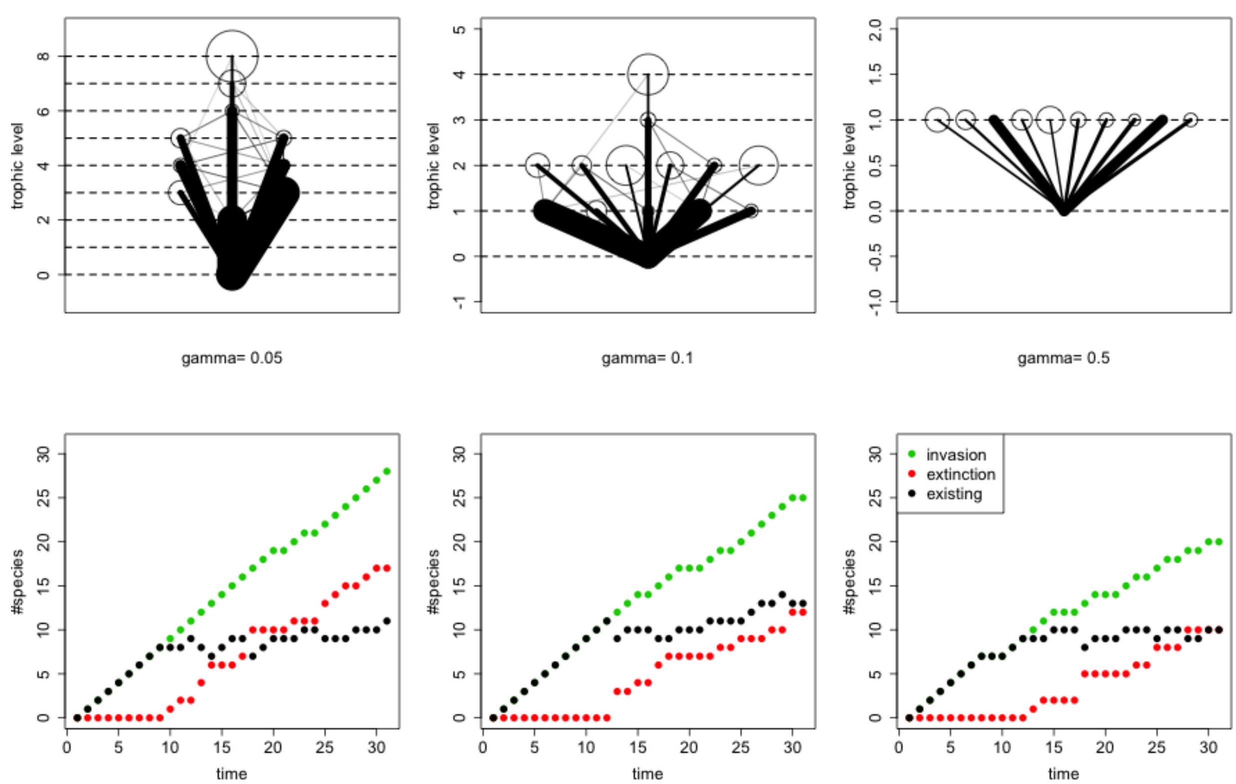

Fig. 4 γ effect when species can feed on other species and resource

simultaneously ($D_r = 0.5$, γ from left to right is 0.05, 0.1 and 0.2)

Again γ does not much affect the number of species, but its negative effect on the number of trophic links is further manifested.

3 Discussion

From the way food web is assembled in this model, the fundamental resource is more naturally interpretable as plant while all invading species as animal (so that a plant can never be predator). In real world there are of course species feeding on both plants and animals, but there is probably extra cost for extending predation from animal-only to animal plus plant, much higher than the cost for extending to another animal species. This suggests that the actual pattern should probably be in between the above two scenarios, and that the cost function ($\tau_c = e^{-\gamma \sum D_{r,p}}$ must be improved to involve not only within-species variation of the preys ($D_{r,p}$) but also between-species variation among them (the latter should get much bigger than the former when plant is included into food source).

Our results show that when the species are allowed to feed on the resource and other species at the same time, despite of a positive $D_{r,R}$ (and therefore cost in capture efficiency τ_c), they all tend to feed on the resource whether or not they feed on other species. Three simplest reasons among all: first, the resource contains the most energy and therefore is a highly favorable food source; second, as mentioned earlier, there is probably extra cost in having both plant and meat as food that has not been accounted for here; third, we have assumed all species to have the same D_r, making them equally competitive (when having the same θ) in competing for the same resource. If instead species have differential D_r, those with high D_r might be better off consuming only on other species but not the fundamental resource. This can be tested in the future.

To address another interesting point, cannibalism is implicitly included in this model since if a species from the pool invades the community more than once, later invaders could potentially choose to prey on individuals of the same species that invaded earlier. It might be challenging to quantify this behavior since it depends on the number of times a species can invade the community, in addition to all other existing parameters. The key point is that cannibalism can happen in this framework if the same species can invade multiple times, e.g. when the invading species is sampled from the pool with replacement.

A Link-species relationship for the above two cases

Since the new algorithm is very slow (the searching for optimal prey set is expanded to all other species) and LSR requires a gradient of resource availability, here I only give preliminary comparison within very restricted ranges for all parameters so that it does not take more than a few hours to run.

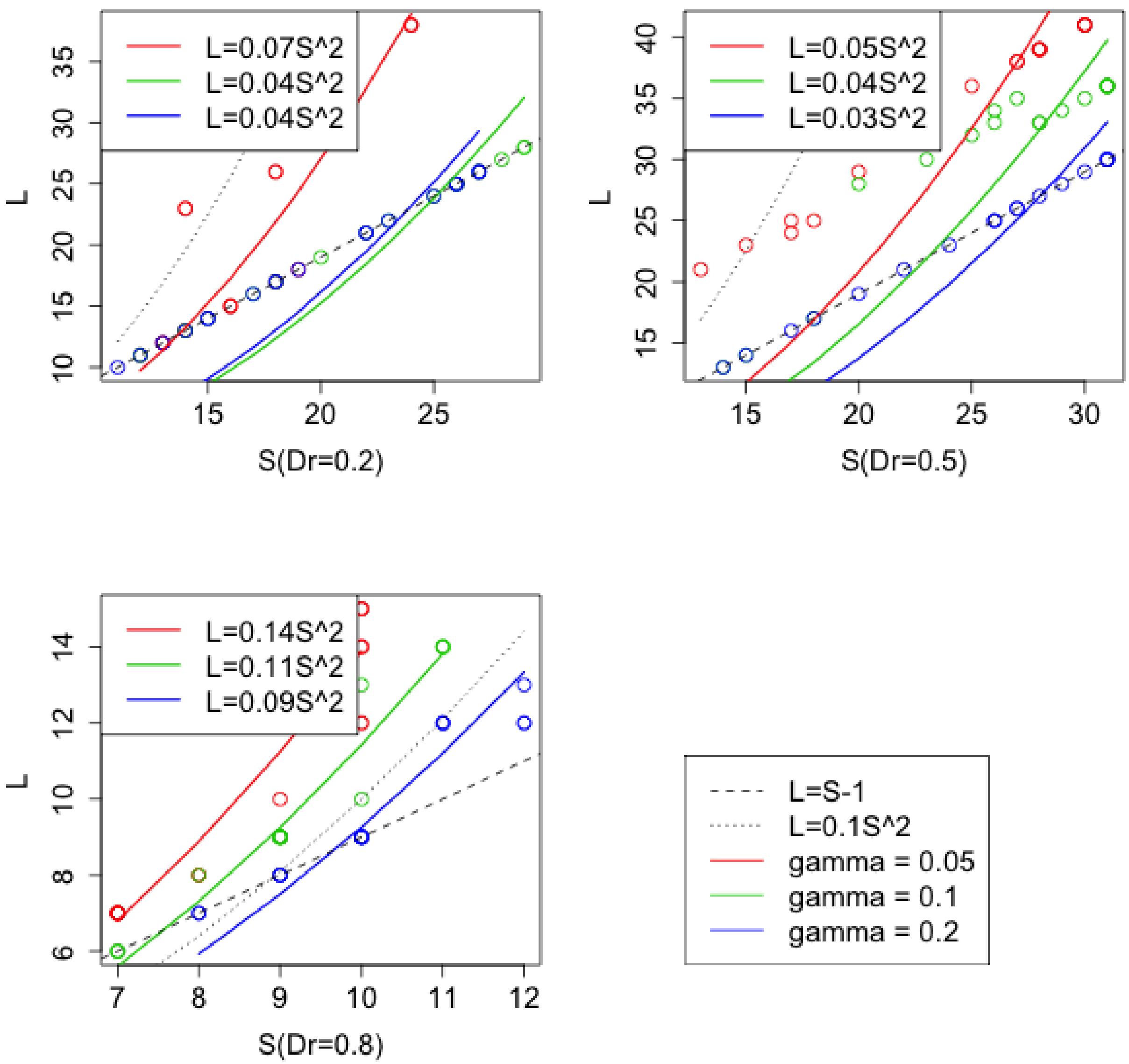

Fig. A - 1 Link-species relationship for the first case (Section 1)

$\tau_u = 0.1$

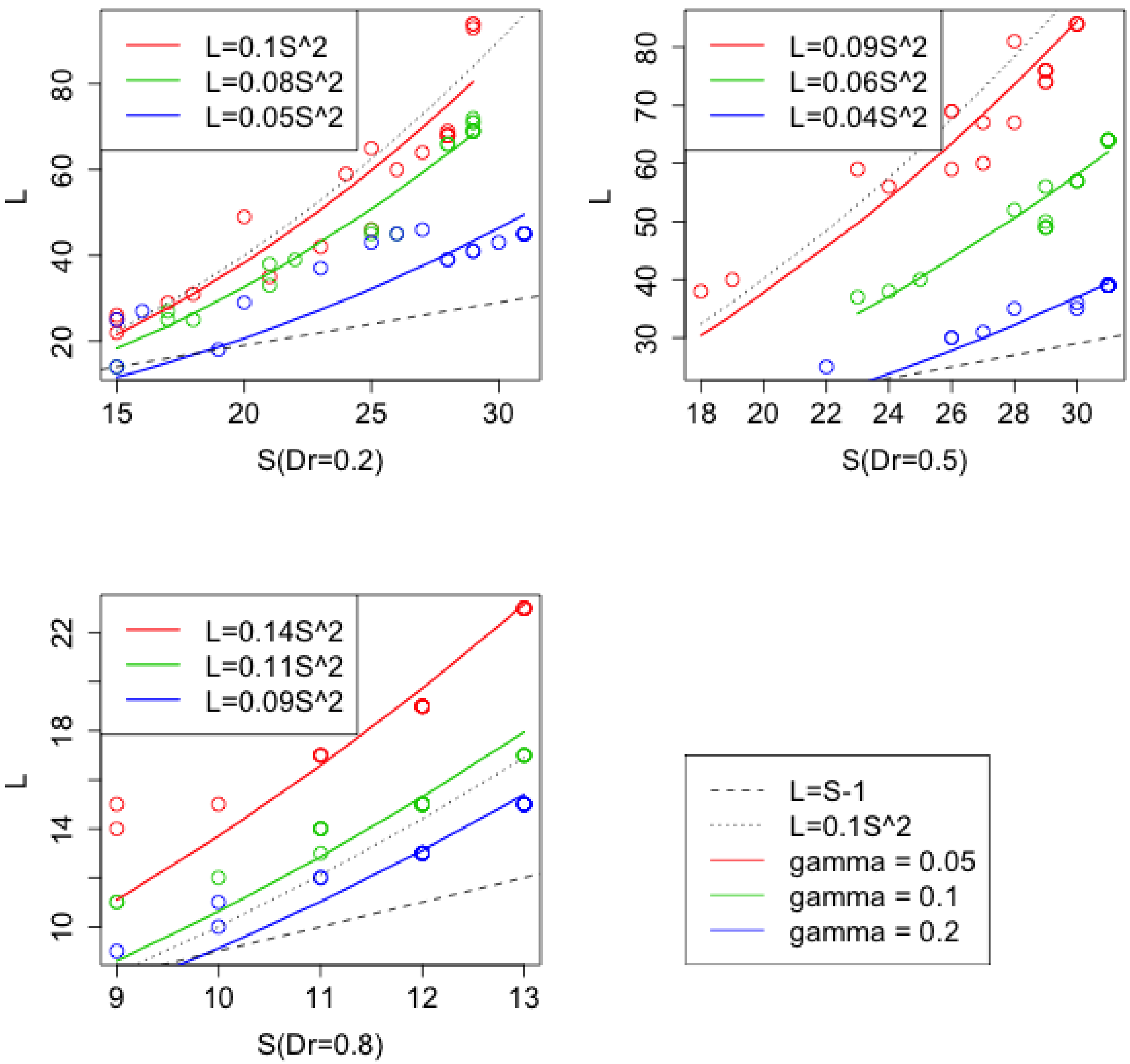

Fig. A - 2 Link-species relationship for the first case (Section 1)

$\tau_u = 0.2$

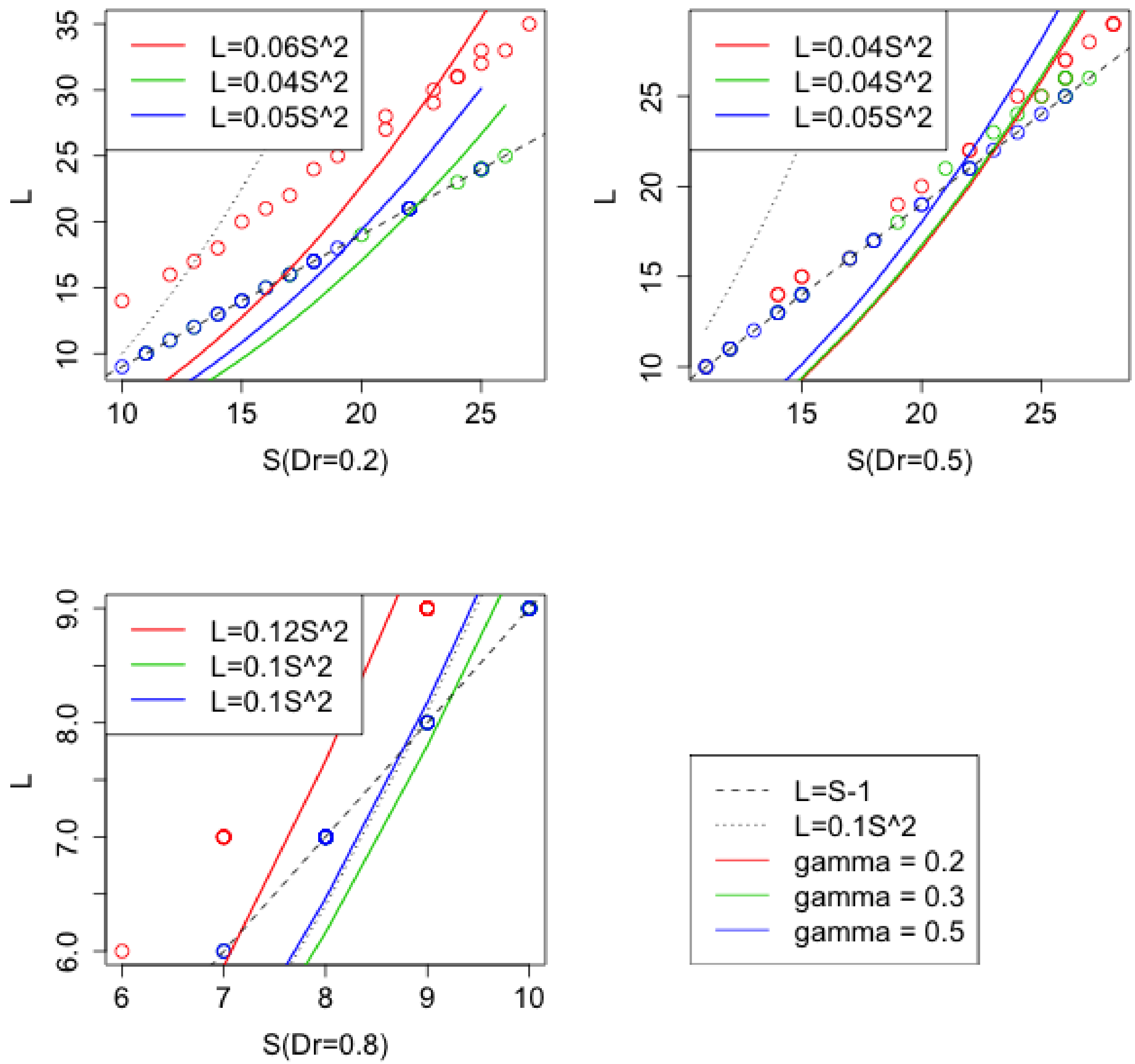

Fig. A - 3 Link-species relationship for the second case (Section 2) $\tau_u = 0.1$

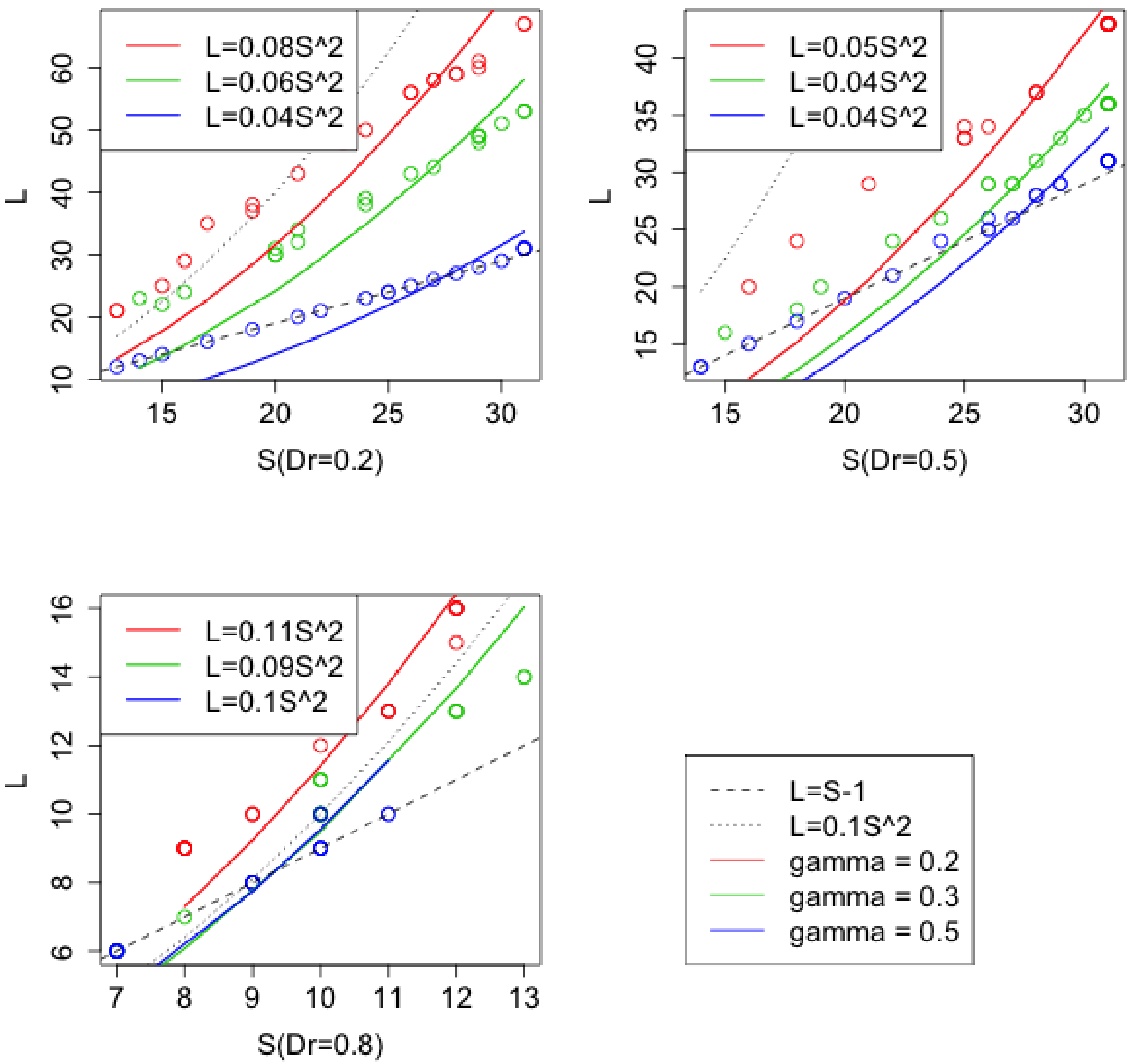

Fig. A - 4 Link-species relationship for the second case (Section 2) $\tau_u = 0.2$

In both cases, the higher the γ, the smaller the coefficient c in $L = cS^2$ and the closer LSR is to its lower boundary ($L = S - 1$); the effect D_r is nonlinear, with $D_r = 0.8$ giving the highest estimate for c, $D_r = 0.5$ the lowest and $D_r = 0.2$ intermediate; the higher the utilization efficiency τ_u, the higher the estimate for c (more significantly for lower D_r).

For the same parameter setting ($\gamma = 0.2$, the blue curve in Fig. A-1 and A-2 and the red curve in Fig. A-3 and A-4), the second case gives higher estimate for c, which is understandable since the second case allows species to prey on species and resource at the same time which increases the number of potential trophic links for a given number of species. More worth noticing is that for all parameter settings, LSR seems to be a straight-line for the second case while more quadratic for the first case. This might provide some insights into what constraints or factors lead to patterns that better fit trophic scaling rule (linear LSR) or constant connectance (quadratic LSR).